

## Seed caching and cache pilferage by three rodent species in a temperate forest in the Xiaoxinganling Mountains

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**Abstract:** Although differences in food-hoarding tactics both reflect a behavioral response to cache pilferage among rodent species and may help explain their coexistence, differentiation in cache pilfering abilities among sympatric rodents with different hoarding strategies is seldom addressed. We carried out semi-natural enclosure experiments to investigate seed hoarding tactics among three sympatric rodent species (*Tamias sibiricus*, *Apodemus peninsulae* and *Clethrionomys rufocanus*) and the relationship of their pilfering abilities at the inter- and intraspecific levels. Our results showed that *T. sibiricus* exhibited a relatively stronger pilfering ability than *A. peninsulae* and *C. rufocanus*, as indicated by its higher recovery rate of artificial caches. Meanwhile *A. peninsulae* showed a medium pilfering ability and *C. rufocanus* displayed the lowest ability. We also noted that both cache size and cache depth significantly affected cache recovery in all three species. *T. sibiricus* scatter-hoarded more seeds than it larder-hoarded, *A. peninsulae* larder-hoarded more than scatter-hoarded, and *C. rufocanus* acted as a pure larder-hoarder. In *T. sibiricus*, individuals with lower pilfering abilities tended to scatter hoard seeds, indicating an intraspecific variation in hoarding propensity. Collectively, these results indicated that sympatric rodent species seem to deploy different food hoarding tactics that allow their coexistence in the temperate forests, suggesting a strong connection between hoarding strategy and pilfering ability.

**Keywords:** Caching pilfering; Hoarding strategy; Sympatric rodents; Coexistence

How similar species coexist on similar resources has been a longstanding interest to community ecologists (Randall, 1993; Schoener, 1986). At present, the factors that influence species coexistence are poorly understood, especially among the terrestrial food-hoarding rodents. Several rodent species which are superficially alike in appearance and habit seem to coexist despite relying on the same limited food sources (Chang & Zhang, 2011; Kotler & Brown, 1988). Potentially, behavioral differentiations at the intraspecific or interspecific level may function as a mechanism to facilitate this kind of coexistence (Ben-Natan et al, 2004; Perri & Randall, 1999).

Food hoarding is an evolutionary adaptation that allows animals to manipulate food availability both spatially and temporally (Vander Wall, 1990), thereby increasing chances of survival and reproductive success during periods of food shortage (Post et al, 2006). Jenkins & Breck (1998) and Price et al (2000) predicted that differences in food hoarding strategies among rodent species may allow or facilitate their coexistence. Animals usually store food in two different ways in terms of the

spatial distribution of the stored items: larder-hoarders store large quantities of food in central locations, e.g., burrows, while scatter-hoarders distribute small caches of food items in numerous shallow pits within their home range (Jenkins & Breck, 1998; Vander Wall, 1990). Each strategy is not without risks. Larders, for instance, are vulnerable to catastrophic loss if the individual fails to defend the resources from intraspecific or interspecific pilferers (Dally et al, 2006; Stapanian & Smith, 1978; Vander Wall & Jenkins, 2003). In theory, scatter-hoarding is supposed to reduce this risk (Leaver, 2004; Stapanian & Smith, 1978, 1984; Vander Wall, 1990), but it involves a greater input of energy to recover the scattered caches (Male & Smulders, 2007; Stapanian & Smith, 1978; Vander Wall, 1990, 2000). Similarly, much like larders, scatter-hoards are pilfered by sympatric competitors (Leaver, 2004; Leaver & Daly, 2001; Preston

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& Jacobs, 2001; Vander Wall & Jenkins, 2003). Therefore, pilfering is common and regarded as an alternative foraging strategy adopted by rodents and birds (Dally *et al.*, 2006; Iyengar, 2008; Vander Wall & Jenkins, 2003) and may greatly influence on the respective hoarding strategies of different animals.

Based on the assumption that pilfering can be considered an alternative foraging strategy that then impacts hoarding strategies, it seems likely that species would diverge in their abilities to exploit different food hoarding tactics in order to coexist. Unfortunately, food hoarding tactics of coexisted species are seldom studied (but see Leaver & Daly, 2001; Price & Mittler, 2003; Vander Wall *et al.*, 2009). Here, we investigated the pilfering abilities and hoarding strategies of three small rodent species coexisting in a temperate forest (*Tamias sibiricus*, *Apodemus peninsulae* and *Clethrionomys rufocanus*). The three rodent species rely on seasonally abundant seeds from local tree species *Pinus koraiensis*, *Corylus mandshurica*, *Corylus heterophylla*, and *Quercus mongolica* as their main food supply (Yi & Zhang, 2008; Yi *et al.*, 2011a, b). *A. peninsulae*, a nocturnal species, mainly larder-hoard but seldom scatter-hoard seeds. Another nocturnal species *C. rufocanus* acts as a pure larder-hoarder, though their food mainly consists of roots and bark (Yi, personal observation, data not published). Meanwhile, the Siberian chipmunks, *T. sibiricus*, are a diurnal rodent species and mainly scatter-hoard seeds (Yang *et al.*, 2012a, b; Yi *et al.*, 2011a, b). Our aim was to test two hypotheses: 1) Coexisting species relying on the same limited seed sources may display different hoarding strategies; 2) Unlike larder-hoarders, scatter-hoarders make small caches of food items throughout their home range, and are expected to rely more on spatial memory and olfaction to recover their scattered caches, and accordingly rodent species performing different hoarding strategies should exhibit different pilfering abilities.

## MATERIALS AND METHODS

### Study site

The study was conducted in the semi-natural enclosures in northeastern China at the Dongfanghong Forestry Center (average elevation 750 m, located at N46°50'–46°59', E128°57'–129°17') in Dailing district, Yichun city, Heilongjiang Province. The climate of the experimental site is dominated by northern temperate zonal monsoons with long, severe winters and short summers. The annual average air temperature is 14 °C with a maximum of 37 °C and minimum of –40 °C. Average annual precipitation averages 660 mm, 80% of which falls in the short growing season from May to September (Yi & Zhang, 2008). The study site was located in a mixed secondary broad-leaved and mixed

conifer forest. In the experimental region, common tree species include *Betula platyphlla*, *Juglans mandshurica*, *Quercus mongolica*, *Pinus koraiensis*, *Fraxinus mandshurica*, *Phellodendron amurese*, *Acer mono* and *Tilia amurensis*; beneath the tree canopy, common shrubs are *Corylus mandshurica*, *Corylus heterophylla*, *Fructus schisandrae* and *Acanthopanax senticosus*.

### Establishment of enclosures

We conducted experiments in separate 10 m×10 m semi-natural enclosures that had been previously established in an open and level area. The enclosures were built using 3 m tall bricks placed in the ground, with about 2.5 m high above ground and 0.5 m below the soil surface. The walls of the enclosures were smoothed to prevent escape of small rodents. To prevent predators from entering the enclosures from outside, the enclosures were covered with plastic nets on the top. To allow animals to rest and drink freely, an artificial nest area was constructed of bricks (H×W×L: 20 cm×15 cm×30 cm) in one corner of the enclosure and provisioned with a water bowl. A seed station of 1 m<sup>2</sup> was established at the center of each enclosure.

### Capture of rodent species

Steel frame live traps (H×W×L: 9 cm×10 cm×25 cm), baited with peanuts and carrot, were placed in the forest at 5 m intervals along four transects at 09:00. We checked the live traps every 3 h to ensure the safety of the captured rodents. The animals captured in each visit were transported by vehicle to the laboratory housing room within 30 min. All traps were then taken back at 18:00 and re-placed in the forest the following day. Trapping stopped on days with bad weather, i.e., heavy raining. Rodents transported to the laboratory were kept individually in steel frame cages (H×W×L: 40 cm×50 cm×90 cm) at a natural temperature (15–25 °C) and photoperiod (14 h of light). All specimens were provided with carrots, peanuts, tree seeds and water *ad libitum*. No animal died during the trapping and laboratory feeding processes. In total, we collected 23 specimens including *T. sibiricus* (*n*=7), *A. peninsulae* (*n*=9) and *C. rufocanus* (*n*=7) with respective mature body masses of 104.80±9.25 g, 26.83±5.64 g and 33.38±3.57 g (mean±SD).

### Seed hoarding tactics

We used Korean pine (*P. koraiensis*) seeds because they are seasonally abundant and the most important food sources of all three rodent species. *P. koraiensis* produces medium-sized seeds (L×W: 1.60 cm×1.11 cm; fresh weight: 0.73±0.05 g) that are characterized by low tannin and high caloric value (Yang *et al.*, 2012a). Seeds were labeled with plastic tags according to the previously published method (Yi & Zhang, 2008) with minor

modifications. A hole 0.3 mm in diameter was drilled through the husk, far from the embryo of each seed, without damaging the cotyledon and the embryo. A flexible plastic tag (2.5 cm×3.5 cm, <0.3 g) was tied through the hole in each seed using a thin steel thread, 10 cm long. Seed placement was based on the daily consumption of the three rodent species. For *T. sibiricus*, 30 intact tagged Korean pine seeds were placed at the seed station in each enclosure only once at 07:00 and seed fates were checked at 18:00. For *A. peninsulae* and *C. rufocanus*, 20 seeds were supplied at 18:00 and seed fates were checked in the next morning (08:00). Seed fates were defined using the following abbreviations: intact in situ (IS), eaten in situ (EIS), eaten after removal (EAR), intact after removal (on surface) (IAR), scatter-hoarded (SC) and larder-hoarded (LC). Larder-hoarded seeds were defined as those carried into the artificial nests or belowground nests, while scatter-hoarded seeds referred to those buried in small pits on the surface of ground. In total, we tested 14 *T. sibiricus* (6♀, 8♂), 8 *A. peninsulae* (4♀, 4♂) and 7 *C. rufocanus* (4♀, 3♂) individuals in hoarding trials. Animals were given the opportunity to bury seeds in the enclosures.

### Cache pilfering

To test the pilfering abilities of the three rodent species, the same combination of artificial caches was provided. We established 9 categories of caches in each semi-natural enclosure that differed both in burial depth (1 cm, 2 cm or 5 cm) and the number of Korean pine seeds (1, 2 or 5): 1 seed at 1 cm, 2 cm, and 5 cm; 2 seeds at 1 cm, 2 cm, and 5 cm; and 5 seeds at 1 cm, 2 cm, and 5 cm. Each category was replicated six times, making for a total of 54 caches with 144 seeds in each enclosure. Caches of the same category were spaced more than 2 m apart, and caches of different categories were more than 80 cm apart randomly and evenly distributed in each enclosure. This array of cache categories is supposed to represent actual caches in the field according to burial depth and cache size (Yi et al, 2008). To minimize the influence of artificial clues, each individual of the three rodent species was introduced into the enclosures three days after cache preparation. In the first trial round, 15 *T. sibiricus* (7♀, 8♂) were simultaneously put into 15 enclosures for daytime testing. In the second round, 8 *A. peninsulae* (4♀, 4♂) and 6 *C. rufocanus* (3♀, 3♂) were introduced at night. We provided water but no food other than the experimental seeds. Two days later, we surveyed the enclosures to determine which caches were removed. Removed caches were termed as those that one or more seeds were excavated by rodents.

To further test whether there was an intraspecific variation in pilfering ability of *T. sibiricus*, we randomly selected 32 *T. sibiricus* (17♀, 15♂) and provided them with 30 pine seeds at the seed station of each enclosure every morning. In the afternoon, all seeds and seed

debris were cleaned and the proportion of cached seeds was recorded for four consecutive days. After the four days, the 10 individuals (5♀, 5♂) of both the highest ( $\geq 30\%$ ) and lowest ( $\leq 3\%$ ) caching propensity (termed as the proportion of cached seeds) were selected for further analysis via pilfering trials. We established three categories of caches in each enclosure: 1 seed at 1 cm, 2 cm, and 5 cm deep. Each type of cache was replicated 30 times, for a total of 90 caches (90 seeds) in each enclosure. One individual of each group was introduced in each enclosure in the morning. The number of caches that were removed was checked two days later.

Following the experiments, all animals were released to the site of their initial capture. The trapping and housing of animals were permitted by the Henan University of Science and Technology (No. HAUST015).

### Data analysis

We used SPSS 16.0 (SPSS inc., Chicago, USA) for data analysis. Three-way ANOVA was used to see the effects of rodent species, cache size, and cache depth on the removal rates of artificially cached seeds. Differences in the number of scatter-hoarded seeds selected by the chipmunks with different caching propensity were detected using general linear models (GLM). Difference in the proportion of scatter- and larder-hoarded seeds by the three rodent species was also tested using GLM. Data were arc-sin transformed before analyses.

## RESULTS

Our results indicated that *A. peninsulae* both scatter-hoarded and larder-hoarded Korean pine seeds, with more seeds being larder-hoarded ( $F_{1,14}=13.39$ ,  $df=1$ ,  $P=0.003$ ). *T. sibiricus*, meanwhile, scatter-hoarded more seeds than it larder-hoarded ( $F_{1,26}=24.69$ ,  $df=1$ ,  $P<0.001$ ). *C. rufocanus* did not scatter-hoard at all; instead, it acted as a pure larder-hoarder (Figure 1).

The three rodent species displayed different abilities

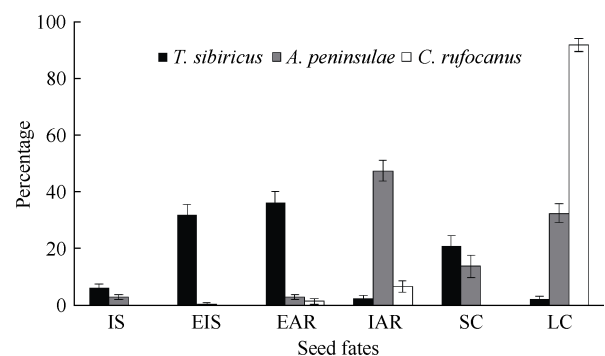


Figure 1 Seed fates manipulated by three sympatric rodent species in semi-natural enclosures

Abbreviations: IS: intact in situ; EIS: eaten in situ; EAR: eaten after removal; IAR: intact after removal; SC: scatter-hoarded; and LC: larder-hoarded. Data are expressed as mean±SE.

to pilfer Korean pine seeds from artificial caches ( $F_{2,8}=178.83$ ,  $P<0.001$ ). *T. sibiricus* exhibited a stronger pilfering ability than *A. peninsulae* and *C. rufocanus* ( $P<0.05$ ). *A. peninsulae* excavated more caches than *C. rufocanus* ( $P<0.001$ ) (Figure 2). Pilfering abilities of the three rodent species decreased dramatically with the

depth of artificial caches ( $F_{2,8}=45.289$ ,  $P<0.001$ ). Seeds at 5 cm deep caches were less likely to be removed than those at 1 and 2 cm ( $P<0.05$ ). Cache size also was found to influence removal rates ( $F_{2,8}=3.67$ ,  $P=0.027$ ), caches containing 5 seeds were more likely to be pilfered than those with 1 or 2 seeds ( $P<0.05$ ) (Figure 2).

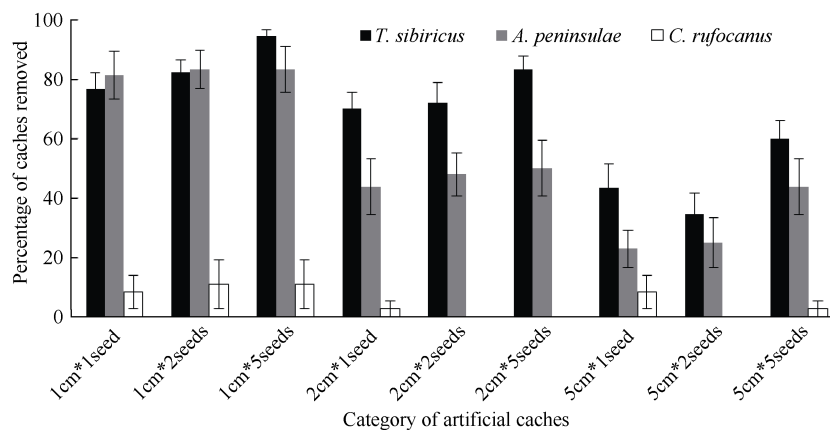


Figure 2 Number of caches excavated by three sympatric rodent species at nine combinations of cache sizes in semi-natural enclosures

Data are expressed as mean $\pm$ SE. Error between replicate single individuals of each species was tested individually.

**Table 1** Cache recovery rates in response to variations in cache size, cache depth, and rodent species

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	861.175 <sup>a</sup>	26	33.122	21.036	0.000
	1 456.732	1	1456.732	925.181	0.000
Cache size	11.558	2	5.779	3.670	0.027
Cache depth	142.620	2	71.310	45.289	0.000
Rodent species	563.149	2	281.575	178.830	0.000
Cache size $\times$ Cache depth	4.203	4	1.051	0.667	0.615
Cache size $\times$ Rodent species	9.457	4	2.364	1.502	0.202
Cache depth $\times$ Rodent species	56.951	4	14.238	9.042	0.000
Cache size $\times$ Cache depth $\times$ Rodent species	3.243	8	0.405	0.257	0.979
Error	368.442	234	1.575		
Total	3 694.000	261			
Corrected Total	1 229.617	260			

<sup>a</sup> R-Squared=0.700 (Adjusted R-Squared=0.667).

We found an apparent intraspecific differentiation in caching propensity of *T. sibiricus* (Figure 3). 19/32 individuals actively scatter-hoarded Korean pine seeds, whereas 13 either seldom or did not scatter-hoarded at all ( $F=37.34$ ,  $df=1$ ,  $P<0.001$ ) (Figure 3). Interestingly, *T. sibiricus* individuals that actively cached exhibited a low ability to pilfer seeds from artificial caches. However, chipmunks that seldom cached seeds removed

significantly more seeds from artificial caches ( $F=13.92$ ,  $df=1$ ,  $P<0.001$ ) (Figure 3). Cache depth did not alter the removal rates by chipmunks ( $F=1.102$ ,  $df=2$ ,  $P=0.339$ ). We also found that individuals of *T. sibiricus* that did not cache tended to immediately eat the seeds they recovered from artificial caches ( $F=16.02$ ,  $df=1$ ,  $P<0.001$ ) (Figure 3).

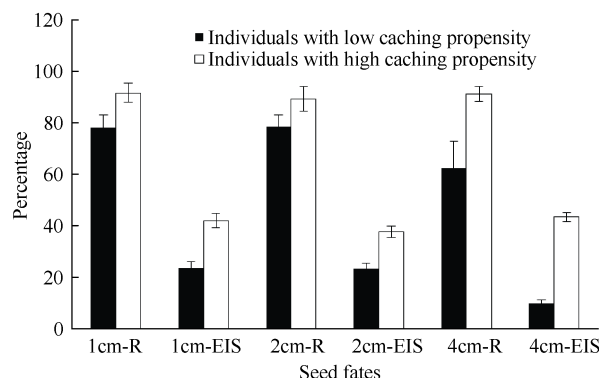


Figure 3 Number of caches excavated by active and inactive caching Siberian chipmunks at three cache depths in semi-natural enclosures

Abbreviations: R: removed; EIS: eaten *in situ*. Data are expressed as mean $\pm$ SE.

## DISCUSSION

Differentiation in food hoarding strategies among coexisting rodent species has been found in other ecosystems (Price & Mittler, 2003; Lu & Zhang, 2008;

Vander Wall et al, 2009; Chang & Zhang, 2011; Huang et al, 2011) and is considered as an adaptation to coexistence (Jenkins & Breck, 1998; Price et al, 2000; Vander Wall, 2000; Leaver & Daly, 2001). In the present study, we found a significant interspecific variation in food hoarding strategies among individuals of all three sympatric rodent species. *T. sibiricus* and *A. peninsulae* exhibited both scatter-hoarding and larder-hoarding, while *C. rufocanus* completely larder-hoarded. *T. sibiricus* and *A. peninsulae* mainly rely on seeds of several local tree species and have an overlap of food niches (Yi & Zhang, 2008), and show a similar hoarding strategy foraging on the other local seed species (unpublished data). Our results further support the idea this kind of differentiation in food hoarding strategies may allow or facilitate the coexistence of sympatric rodent species by reallocating of food resources along an axis of resource heterogeneity (Kotler & Brown, 1988).

As earlier studies have noted, both larder- and scatter-hoarding suffer some disadvantages, such as substantial cache loss and increased costs of food handling (i.e., harvested seeds are transported and cached, then dug up and eaten) (Vander Wall, 1990). Accordingly, the evolution of the mechanism underlying the two hoarding tactics remains uncertain. Andersson & Krebs (1978) suggested that hoarding behaviors evolve when the caching individual is more likely than any other to gain access to their caches. However, more recent studies have noted that rodents significantly increase the intensity of scatter-hoarding but not larder-hoarding when faced with complete cache loss of scatter-hoarded seeds (Huang et al, 2011, but see Preston & Jacobs, 2001). Only a few studies have delved further and investigated the connected behaviors involved in interspecific differences of pilfering abilities (Leaver & Daly, 2001; Thayer & Vander Wall, 2005). Our results showed that rodent species with strong pilfering ability (*T. sibiricus*) tended to rely on scatter-hoarding seeds rather than larder-hoarding. However, rodent species with extremely weak pilfering ability (*C. rufocanus*) completely larder-hoarded food items in their burrows or nests, likely avoiding pilferage by *T. sibiricus* and *A. peninsulae*. Given this finding, it is plausible that the relatively higher pilfering ability of *T. sibiricus* and *A. peninsulae* constrain *C. rufocanus* in to larder-hoarding seeds. To our knowledge, this may be one of only a few studies to suggest a relationship between hoarding strategy and pilfering ability in small rodents (Vander Wall et al, 2009). We further found that the medium

pilfering ability of *A. peninsulae* may explain its dependence on both scatter-hoarding and larder-hoarding because taking a solely scatter-hoarding or larder-hoarding strategy would subject it to substantial losses of hoarded food by *T. sibiricus* (caches) or *C. rufocanus* (larders). Subsequently, adopting scatter-hoarding combined with larder-hoarding may be a novel way for *A. peninsulae* to cope with these pilfering risks.

Current theories state that food-hoarding tactics can be adaptive if a hoarder has a higher priority than any other animal to retrieve its own caches (Vander Wall & Jenkins, 2003). Although larger species are better able to physically defend a larder (Preston & Jacobs, 2001), *T. sibiricus*, possessing the highest body mass in our comparison, performed scatter-hoarding rather than larder-hoarding. This finding suggests that body size (and by extension, defensive ability) is not always a valid explanation of the selection of scatter-hoarding versus larder-hoarding among sympatric rodent species (Dally et al, 2006).

Cache pilfering occurs not only between different species (Burnell & Tomback, 1985), but also between within them (Heinrich & Pepper, 1998), therefore leading to intraspecific variations of hoarding tactics. Our results concurred with this assessment, as we noted an apparent intraspecific differentiation in hoarding strategies among *T. sibiricus*. Individuals of *T. sibiricus* with lower pilfering ability tended to scatter-hoard more seeds than those who possessed a higher pilfering ability, implying that non-hoarding individuals are common in rodent populations. Individuals of *T. sibiricus* with higher pilfering ability are expected to rely on food resources pilfered from caches of conspecifics or interspecifics. Conversely, individuals with lower pilfering ability tend to perform scatter hoarding tactics and recover their caches mainly through spatial memory. Therefore, scatter hoarding is predicted to be an alternative strategy for individuals with lower pilfering ability to prevent cache losses (MacDonald, 1997; Preston & Jacobs, 2001; Gálvez et al, 2009). In summary, our results indicate that sympatric rodent species seem to deploy different food hoarding tactics that allow their coexistence in the temperate forests, suggesting a strong connection between hoarding strategy and pilfering ability.

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